Past, Present and Future Discovery of the Amazon Tree Flora

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2017

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Rede uitgesproken bij de aanvaarding van het ambt van buitengewoon hoogleraar 'Tropical Forest Diversity and Tree Traits' aan de Faculteit der Aard- en Levenswetenschappen van de Vrije Universiteit Amsterdam op 11 mei 2017 door Prof. Dr. Hans ter Steege.

VU VRIJE UNIVERSITEIT AMSTERDAM

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Mijnheer de Rector, lieve familie, beste collegas, vrienden, dames en heren.

Tropical forests are storehouses of diversity. While they cover just 10% of our earth's surface they may hold 50% of all terrestrial species. The forests and savannahs of the Amazon basin and Guiana Shield (here Amazonia) arguably hold the greatest terrestrial biodiversity: an estimated 1300 species of birds, 427 species of mammals and 50,000 species of seed plants (*1, 2*). Still, plants in the Amazon remain hugely under-collected (*3, 4*) and the challenge of discovering and understanding such an enormous diversity drives my scientific interest.

A personal note

My personal interest for the Amazon arose during my childhood, inspired by reading 'Walt Disney's Wonderen der Wildernis' (*5*). This book described the adventures of jaguars, jaguarundi's, ocelots, monkeys and birds. It also showed the fantastic 'Teatro Amazonas' in Manaus, based on the wealth of the rubber boom, and beautiful floating villages and markets. Also the television series 'Daktari' helped my imagination. The idea of driving around with a Landover in remote areas was a dream.

So I was lucky that in 1985, during my MSc, I had the opportunity to work in the forest in Guyana and study the zonation of vascular and non-vascular epiphytes with Hans Cornelissen, climbing rainforest trees (*6-8*). In 1989 I moved to Guyana to start the 'Forest Project Mabura Hill', a collaboration between the Utrecht University and University of Guyana, and a precursor for the Tropenbos-Guyana Programme, a research and extension programme funded by the Dutch and Guyanese Governments and targeted for wise forest management and conservation in the forests of Guyana (*9*). Here I also carried out the work for my doctoral thesis (*10*).

In 1998 I returned to the Netherlands and focussed again on biodiversity, working on 'Plant diversity in Guyana for the National Protected Areas System' (*11*). It was during this time that I started to explore the use of forest inventories and tree traits for biodiversity research in the Neotropics (*12-14*) and my work expanded into the wider Amazon.

With 5.5 km^2, Amazonia is one of the largest wildernesses on earth. Travel to remote areas there can be arduous and perhaps dangerous but not nearly so as in the days of the early explorers, when many would not return from their trips. In remote areas the forests are teeming with wildlife. While some emphasize the dangerous wildlife (jaguars, caiman, snakes, spiders), I see mainly beauty in the forest: fantastic landscape, towering trees, beautiful flowers, cauliflory (flowers on trunks), epiphytes, saprophytes (now mycoheterotrophs), lianas and much more.

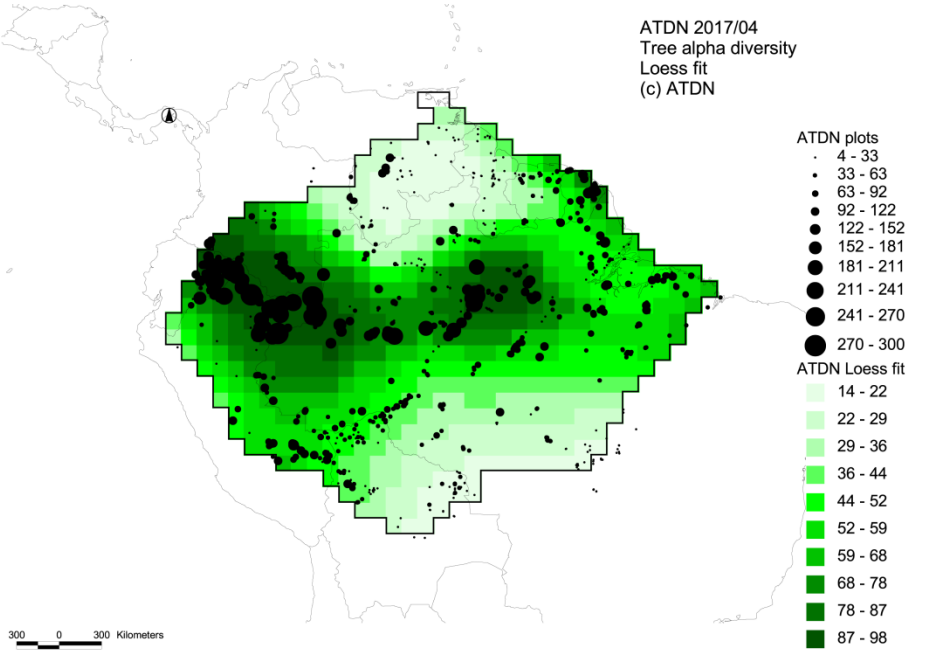

Figure 1. Map of tree α-diversity of the Amazon (http://atdn.myspecies.info), based on a loess interpolation of Fisher's α of 2032 plots of mostly 1-ha. Black dots: Fisher's α of individual plots. Green background colour: the interpolated values calculated for 565 Amazonian 1-degree grid cells.

The Amazon Tree Diversity Network (ATDN)

The publication of Terborgh and Andresen (*15*), arguably, sparked the start of a network of tree diversity plots in all of Amazonia. While ATDN started with a modest amount of contributors (*16*), it has grown steadily over the years. The first goal was to describe, map, and understand the diversity of the forests. The first maps of diversity was produced in 2000 (*16*), with an new version in 2003 (*17*) and we have updated a web version since (Fig. 1; http://atdn.myspecies.info).

At this moment ATDN has 200 contributing members and 2032 plots (Fig. 2), 1751 of which with composition data. ATDN is our tool to try to understand the bewildering diversity of the Amazon. Questions we ask are (a.o.): how many trees are there; how many species; what is the geographical structure; what are their populations; who is common, who is rare, and why; what are their traits; what is their function; what is the history/evolution; what are the threats?

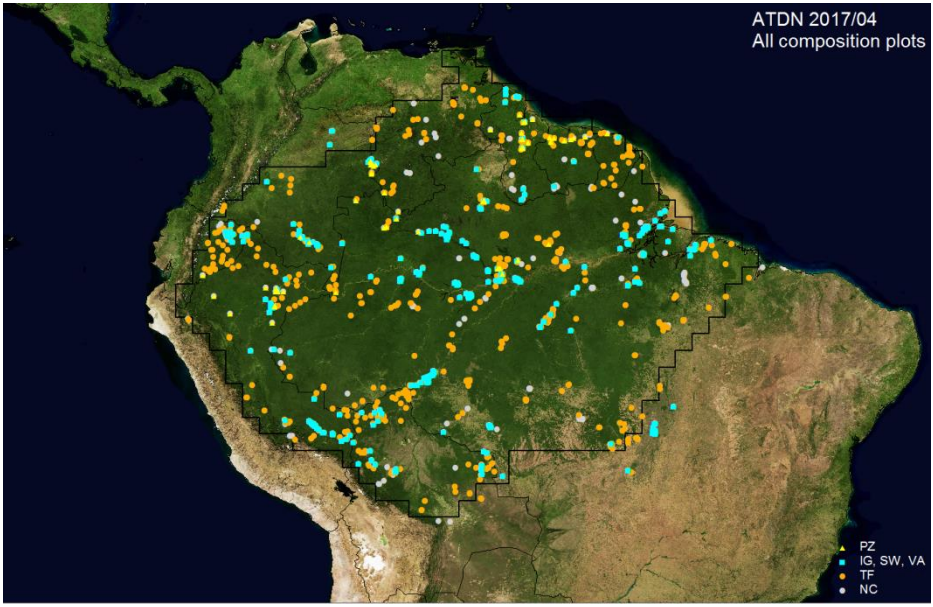

Figure 2. Map of Amazonia showing the location of the 2032 Amazon Tree Diversity Network (ATDN) plots. The black polygon marks our delimitation of the study area and consists of 567 1° grid cells (area = 6.29 million km2). Coloured dots: plots with composition. Orange circles indicate plots on terra firme; blue squares, plots on seasonally or permanently flooded terrain (várzea, igapó, swamps); yellow triangles, plots on white-sand podzols; gray circles, plots only used for tree density calculations. Background is from NASA Visible Earth.

At the core of all those questions are the mechanisms determining the biological diversity of ecosystems. Ecologists and evolutionary biologists study diversity at different scales and what has become clear is that scale is an important bridging element between theories. In short, diversity is influenced by regional as well as local processes (*18, 19*), all operating at specific space and time-scales (Fig. 3).

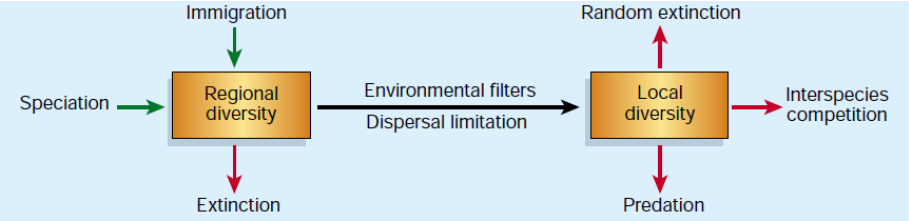

Figure 3. Determinants of biodiversity (*20*). Impacts on diversity occur at both regional and local scales (*18, 21*): here, green arrows indicate processes that increase diversity (species are added) and red arrows those that decrease it (species are lost). Regionally, diversity is mainly influenced by speciation and extinction and, to a certain extent, by immigration. These processes determine the number of regional species from which local communities can 'draw' particular species. Of course not all species can occur everywhere, either because the habitat is unsuitable (environmental filters) or because of constraints on their movement (dispersal limitation).

Despite the biological and societal importance and the large scientific effort trying to understand the origins of biodiversity the question 'what determines species diversity' is still among the 25 most important science questions (*22, 23*). Mechanisms generating and regulating diversity have been a central theme in my research (and teaching) and the model of Fig. 3 is often my working model to understand and study biodiversity. The model can run from a complete neutral model (with only the factors speciation, extinction, dispersal and random extinction operating), to island biogeography (local diversity, only dispersal and random extinction operating), to a full niche model (with environmental filtering, competition and predation operating). We have successfully used this model to separate the regional and local signal in tree alpha-diversity in the Amazon, to be able to better understand the causes for variation in each of them (*24, 25*).

A historical perspective of the Amazon (*26*)

The timing of the origin as well as the evolutionary causes of the Amazonian diversity are a matter of debate. The uplift of the Andes and its effect on regional climate fundamentally changed the Amazonian landscape by reconfiguring drainage patterns and creating a vast influx of sediments into the basin. On this "Andean" substrate, a region-wide edaphic mosaic developed that became extremely rich in species, particularly in Western Amazonia. First large salty wetlands dominated western Amazonia and were the habitat for communities of crocodilian species, huge tortoises and many saltwater snails. These wetlands were drained when the uplift of the Andes progressed and the Amazon started to flow eastwards. The birth of the Amazon, indicated by the start of its sedimentary fan was roughly 7 million years ago.

Thus, the Andean uplift was crucial for the evolution of Amazonian landscapes and ecosystems, and that current biodiversity patterns are rooted deep in the pre-Quaternary (*26*).

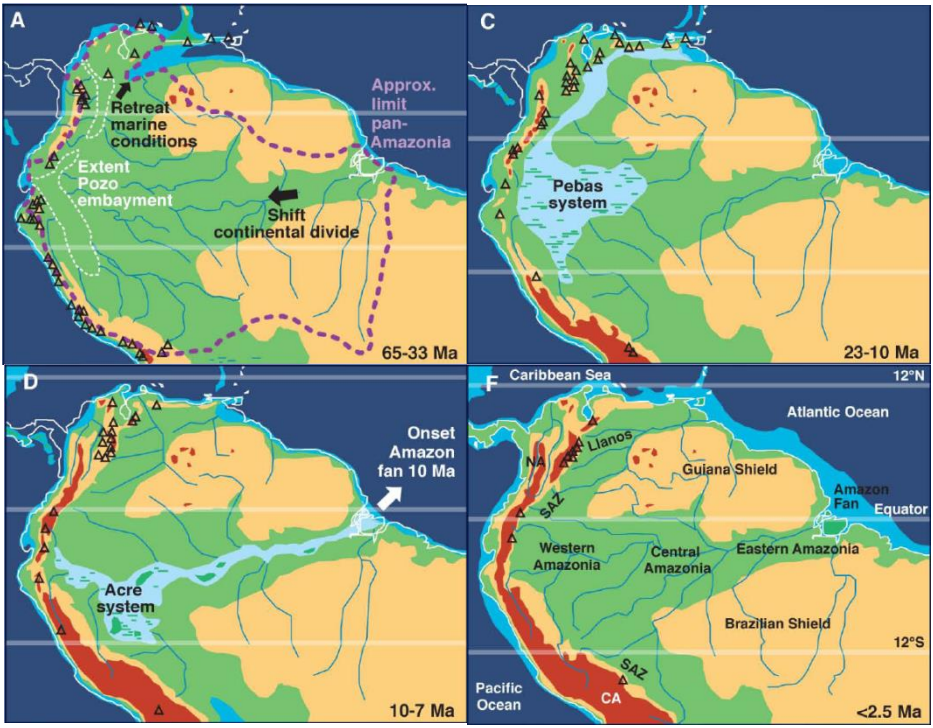

Figure 4. The early Amazon in 4 periods. Paleogeographic maps of the transition from "cratonic" (A) to "Andean"-dominated landscapes (C,D,F). (A) Amazonia once extended over most of northern South America. Breakup of the Pacific plates changed the geography and the Andes started uplifting. (C) Mountain building in the Central and Northern Andes (~12 Ma) and wetland progradation into Western Amazonia. (D) Uplift of the Northern Andes restricted "pan-Amazonia" and facilitated allopatric speciation and extirpation. (F) Quaternary. Note that South America migrated northward during the course of the Paleogene (*26*).

As early as ~60 million years ago Neotropical rainforests flourished, with many palm species, Fabaceae species and family composition similar to current Neotropical rainforest (*27*). Why the Amazon has so many species remains a question (*28*). Haffer's refuge theory (*29*), which posited that during the drier periods in the Pleistocene the Amazon forest has shrunk into so called 'refugia', drivers for speciation, was so elegant and fitting our ideas of allopatric speciation that it took

very long for its falsification to be accepted (*30*). Speciation was likely continuous over long periods with significant species turn-over (*26, 31*). About the most important modes of speciation in the Amazonian flora, discussion is still ongoing. There is support for allopatric speciation (*32*), dispersal driven speciation (*33*) and sympatric/ecological speciation (*34*).

Hyperdominance in the Amazon Tree Flora (*35*)

The vast extent of the Amazon Basin has historically restricted the study of its tree communities to the local and regional scales. Tree inventories carried out over the last two decades have helped improve our understanding of regional-scale patterns of distribution and abundance in Amazonian tree communities, but similar advances at the basin-wide scale remained scarce. Scientists did not know how many tree species occur in the Amazon (*36*), how many tree species have been recorded to date in the Amazon, how those species are distributed across the basin, and in what regions or forest types they are rare or common. So uncertain are patterns at the largest scales that even the simplest question of all — what is the most common tree species in the Amazon?—was never addressed in the scientific literature, much less answered (*35*).

We compiled and standardized species-level data on more than half a million trees in 1170 plots sampling all major lowland forest types to explore patterns of commonness, rarity, and richness (*35*). This provided us with a first accurate estimate of the total number of trees in the Amazon: 3.9×10^{11} trees. As this was actually just a matter of combining tree densities per ha with the total area of the Amazon, this result may seem almost trivial. It turned out, however, that this number was nearly equal to the, then current, estimate of trees world-wide (*37*). Crowther et al (*37*) now estimate the latter at three trillion, 15 billion of which are cut down each year. They also estimate that 46% of all trees may have been cut down in the Anthropocene already.

Based on our 1170 tree plots we estimated the population sizes of 4962 tree species occurring on our plots. We then estimated the total number of tree species in Amazonia by fitting the mean rank-abundance data to a Fisher's log-series distribution (Fig. 4). Our analysis suggests that lowland Amazonia harbors ~16,000 tree species. We found 227 "hyperdominant" species (1.4% of the total) to be so common that together they account for half of all trees in Amazonia, whereas the rarest 11,000 species account for just 0.12% of trees. Most hyperdominants are habitat specialists that have large geographic ranges but are only dominant in one or two regions of the basin, and a median of 41% of trees in individual plots belong to hyperdominants. A disproportionate number of hyperdominants are palms,

Myristicaceae, and Lecythidaceae. At this moment *Eschweilera coriacea* (Lecythidaceae – Brazil nut family), with over 5 billion trees (over 10 cm dbh) is the most common species in Amazonia but *Euterpe precatoria* and *Protium altissimum*, each also with over 5 billion trees are close competitors for this rank.

The causes underlying hyperdominance in these species remain unknown. Both competitive superiority, resistance to pathogens, and widespread pre-1492 cultivation by humans are compelling hypotheses that deserve testing (see below). Although the data suggest that spatial models can effectively forecast tree community composition and structure of unstudied sites in Amazonia, incorporating environmental data may yield substantial improvements. An appreciation of how thoroughly common species dominate the basin has the potential to simplify research in Amazonian biogeochemistry, ecology, and vegetation mapping. Such advances are urgently needed in light of the >10,000 rare, poorly known, and potentially threatened tree species in the Amazon.

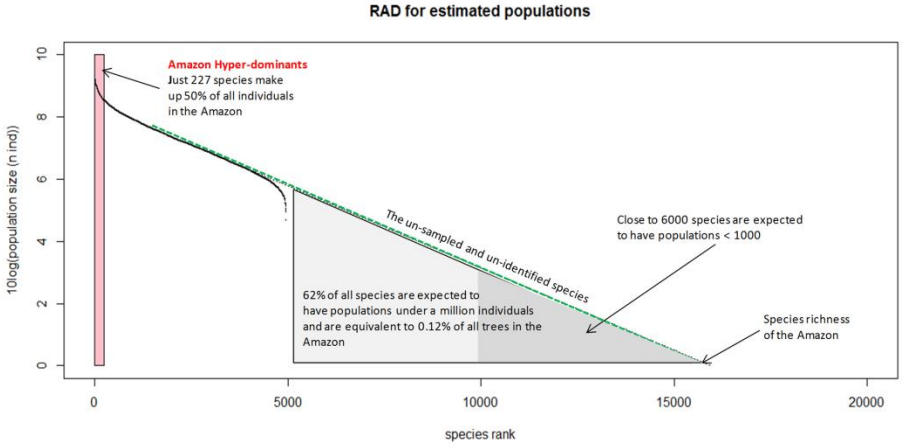

Figure 4. A rank-abundance diagram of 4962 tree species extrapolated to estimate the size of the Amazon tree flora. The mean estimated Amazon-wide population sizes of 4962 tree species are shown as a solid line, and the dotted line is an extrapolation of the distribution used to estimate the total number of tree species in Amazonia (*35*).

We were heavily criticised by one of our reviewers for the use of Fisher's α to obtain an estimate of the total number of species (rather than non-parametric estimators) and others have criticised this approach as well (*38, 39*), while the number has also been embraced as the 'true number' (*40*). Non-parametric estimators (*41*) have been used extensively to estimate species richness but we recently showed that their

assumptions do not meet the way data is being collected in large areas with high species richness (they severely underestimate the richness in the Amazon at 6000-7000 species (*35*)) and that an approach with Fisher's α may actually provide better estimates (*42*). Yet, there appeared to another empirical way to test our estimate – simply counting the collections of trees in the Amazon in Herbaria and other Natural History Museums.

Past discovery of the Amazon Tree Flora (*43*)

To provide a stronger empirical foundation for the debate on species numbers in the Amazon, we provided a preliminary checklist of all valid tree species collected to date in Amazonia (*43*). We also analysed the list to explore why some Amazonian tree species are more frequent in herbaria and other floristic datasets than others. Does a species' frequency in these datasets reflect its abundance and range size, the date it was first discovered in Amazonia, the spatial pattern of Amazonian exploration, or some combination of those factors? Answering these questions allowed us to discuss the dynamic behind the discovery of new species and consequently the best approach to complete the inventory of the Amazonian tree flora.

After sifting through tens of millions of collections (GBIF, SpeciesLink and herbaria not present in these repositories), we reported 530,025 unique collections of trees in Amazonia, collected between 1707 and 2015, for a total of 11,676 species in 1225 genera and 140 families (Fig. 5). These figures supported our estimate of 16,000 Amazonian tree species based on the ecological plot data. Botanical collection in Amazonia is characterized by three major peaks, centred around 1840, 1920, and 1980, which are associated with flora projects and the establishment of inventory plots. Most collections were made in the 20th century. The number of collections has increased exponentially, but shows a slowdown in the last two decades. We found that a species' range size is a better predictor of the number of times it has been collected than the species' estimated basin-wide population size. Finding, describing, and documenting the distribution of the remaining species will require coordinated efforts at under-collected sites.

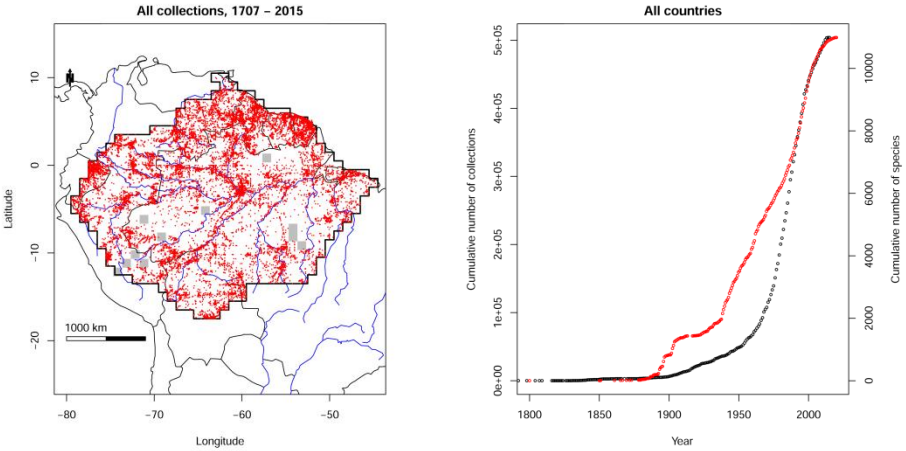

Figure 5. Left: Collection localities of herbarium specimens of Amazonian trees, collected between 1707 and 2015, for which geographical coordinates were available and considered reliable. Map created with custom R script. Base map source (country.shp, rivers.shp): ESRI (http://www.esri.com/data/basemaps, © Esri, DeLorme Publishing Company). **Right**: Cumulative number of tree species specimens collected in Amazonia from 1800 to 2015 (Black line, left y-axis). Cumulative number of tree species collected in Amazonia from 1800 to 2015 (red line, right y-axis) (*43*).

A pristine Amazon? Persistent effects of pre-Columbian plant domestication on Amazonian forest composition (*44*)

The extent to which pre-Columbian societies altered Amazonian landscapes is hotly debated. Our findings suggested that perhaps domestication might have played a role in the dominance of certain species in the Amazon (*35*). To test this idea we performed a basin-wide analysis of pre-Columbian impacts on Amazonian forests by overlaying known archaeological sites in Amazonia with the distributions and abundances of 85 woody species domesticated by pre-Columbian peoples (*44*). Domesticated species appeared five times more likely to be hyperdominant than non-domesticated species, supporting the idea that pre-Columbian people significantly affected Amazonian forest composition. Across the basin, the relative abundance and richness of domesticated species increase in forests on and around archaeological sites. In southwestern and eastern Amazonia, distance to archaeological sites strongly influences the relative abundance and richness of domesticated species. Our analyses suggest that modern tree communities in Amazonia are structured to an important extent by a long history of plant domestication by Amazonian peoples - domestication shaped Amazonian forests. (*44*) but the extent to which this happened will remain a debate for some time to come.

Threats to the Amazon Tree Flora - Estimating the global conservation status of more than 15,000 Amazonian tree species (*45*)

Amazonian forests have lost ~12% of their original extent and are projected to lose another 9-28% by 2050 (*46, 47*). The consequences of ongoing forest loss in Amazonia are relatively well understood at the ecosystem level, where they include soil erosion (*48, 49*), diminished ecosystem services (*50-53*), altered climatic patterns (*50, 52, 54-56*), and habitat degradation. By contrast, little is known about how historical forest loss has affected the population sizes of plant and animal species in the basin, and how ongoing deforestation will affect those populations in the future.

As a result, the conservation status of the >15,000 Amazonian tree species remained unknown. Only a tiny proportion of Amazonian tree species have been formally assessed for the IUCN Red List to date. Two previous studies have attempted to estimate the extinction threat to Amazonian plants using theory, data, and vegetation maps to model reductions in range size, but disagreed on whether the proportion of threatened plant species in the Amazon is low (5-9%) (*57*) or moderate (20-33%) (*36*).

We built on that work by using a spatially explicit model of tree species abundance (*35*) based on 1,485 forest inventories to quantify how historical deforestation across Amazonia (*46, 47, 58*) has reduced the population sizes of 4,953 relatively common tree species (*45*). We used a separate model to estimate population declines for an additional 10,247 rarer tree species (*35*). For both models we also estimated the population losses expected under two deforestation scenarios for 2050 (BAU: business as usual; GOV: improved governance; *46, 47*), and asked to what extent projected losses can be prevented by Amazonia's existing protected area network. In contrast to previous studies, which presented results in the currency of statistical probability of extinction, we analyzed our data using the criteria of the IUCN Red List of Threatened Species, the most commonly used yardstick for species conservation status.

We overlaid spatial distribution models with historical and projected deforestation and showed that at least 36% and up to 57% of all Amazonian tree species are likely to qualify as globally threatened under International Union for Conservation of Nature (IUCN) Red List criteria (Fig. 6). If confirmed, these results would increase the number of threatened plant species on Earth by 22%. We showed that the trends observed in Amazonia apply to trees throughout the tropics, and predicted that most of the world's >40,000 tropical tree species should qualify as globally threatened. A gap analysis suggested that existing Amazonian protected areas and indigenous territories will protect viable populations of most threatened species if these areas suffer no further degradation, highlighting the key roles that protected areas,

indigenous peoples, and improved governance can play in preventing large-scale extinctions in the tropics in this century (*45*).

Our analyses suggest that historical and ongoing forest loss may cause population declines of >30% in one quarter to one half of all Amazonian tree species by 2050. These declines affect species in all Amazonian regions, including iconic Amazonian trees such as Brazil nut (*Bertholletia excelsa*), wild populations of major food crops such as cacao (*Theobroma cacao,* 50% population decline with the BAU) and açai palm (*Euterpe oleracea*, 72% decline with BAU), and 167 of the 227 hyperdominant taxa that account for half of all Amazonian trees (*35*). And while these declines comprise both historical population losses and population losses projected to occur in the future, they could be used to currently classify these species as threatened under IUCN Criterion A4b. Thousands of other Amazonian tree species are likely to qualify as globally threatened because they have very small populations. And while our methods and results are preliminary, the statistical independence we find between the estimated population size of a species and its fractional decline in numbers suggests that the primary findings will remain stable as sampling improves.

Most tropical tree species may be globally threatened

Despite strong spatial clustering in both deforestation scenarios and species distributions, our analyses revealed a simple rule of thumb that works at both regional and basin-wide scales: n% forest loss yields an average ~n% population loss (Fig. 6). This implies that tree species in other forest biomes of tropical South America have lost much larger proportions of their populations than in the core closed-canopy Amazonian moist forest: e.g. the Atlantic Forest (84-88% forest loss) (*59*), the cerrado (53%) (*60*), the caatinga (37%) (*60*), and dry forests in general (>60%) (*61*).

Given that Africa has lost ~55% of its tropical forests and Asia ~35%, mostly since 1900 (*62*), our analyses suggest that most tree species in the Old World tropics have lost more than 30% of their individuals over the last 150 years and thus qualify as globally threatened under Criterion A4. In turn, because >90% of all tree species on Earth are tropical (*63*), trees may deserve to join cycads (63%), amphibians (41%), and corals (33%) on the list of the groups with the highest proportions of globally threatened species.

Although many tropical tree species have symbiotic relationships with animals and co-occur with thousands of species of non-arboreal plants, high rates of threat cannot be inferred for these organisms in the same way, due to their much shorter lifespans. Bird et al. (*64*) compared estimated range maps of Amazonian bird species

with maps of projected deforestation during three bird generations and found that just 5.5–18.8% species qualified as threatened under Criterion A4. Three bird generations in their model averaged 14.8 years, compared to 150 years in our tree model.

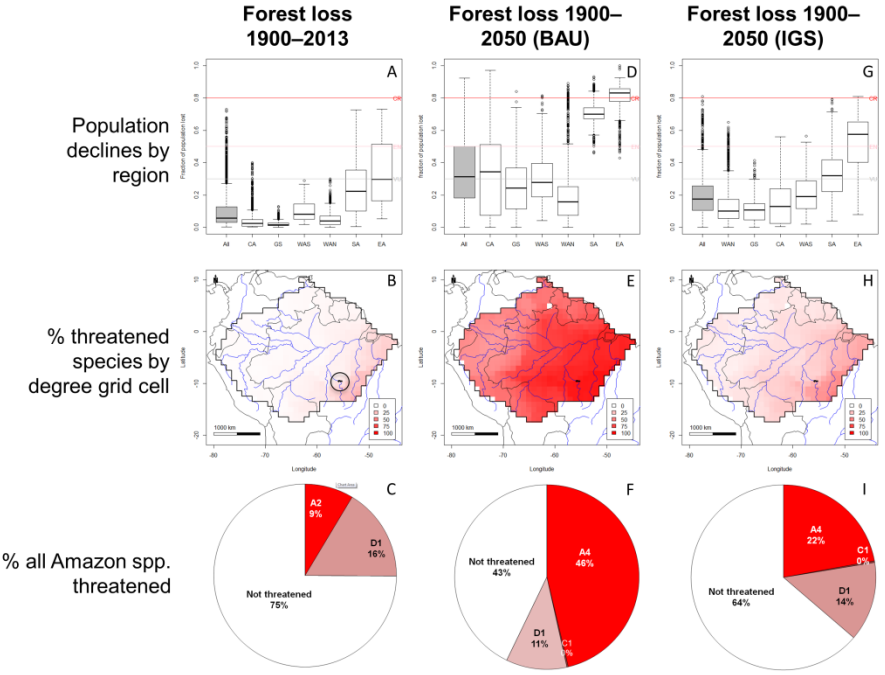

Figure 6. Estimated population declines and threat status of Amazonian tree species under historical deforestation and two projected deforestation scenarios. Historical deforestation (A to C). Projected deforestation (D to I). Top row: Percent population loss of 4953 tree species in the entire Amazon and in six Amazonian regions. Middle row: Percent species in a DGC estimated as globally threatened based on projected (including historical) forest loss (IUCN A2 and A4; n = 4953). Bottom row: Proportion of all 15,200 Amazonian tree species estimated to be globally threatened based on four different IUCN threat criteria. BAU: projected (including historical) deforestation through 2050 based on a BAU scenario (1, 2); IGS: projected (including historical) deforestation through 2050 based on an IGS (1, 2). Cristalino State Park is the small black polygon in southeastern Amazonia, encircled in (B). CA, Central Amazonia; GS, Guiana Shield; WAS, Southwestern Amazonia; WAN, Northwestern Amazonia; SA, Southern Amazonia; EA, Eastern Amazonia; CR, critically endangered; EN, endangered; VU, vulnerable.

Linking forest loss, species threat status, and protected areas management in the Amazon

Heavy forest clearing in southern and eastern Amazonia has put an especially high proportion of tree species there at risk of extinction (Fig. 6A). In the worst-hit areas of the Arc of Deforestation, a third of tree species have already lost >30% of their populations to deforestation and more than half qualify as globally threatened based on projected (and historical) forest loss (Fig. 6B).

By linking spatial trends in forest loss to trends in the population sizes of individual Amazonian plant species in this way, models like ours should soon make it possible to translate remote sensing-based data on Amazonian deforestation into site-specific and species-specific guidance for conservation managers. It will also be possible to model how individual species will be impacted by infrastructure projects (*65*) such as major hydroelectric dams (*66*), degazetting of protected areas (*67*), and other drivers of Amazonian forest loss. This could have serious implications for large-scale development projects, which are increasingly required to protect IUCN-listed taxa and their habitat (e.g., (*68*)).

These models can also generate predictions about which plant species occur in which protected areas, and thus to what extent those species are protected and where. For example, floristic surveys at Cristalino State Park, in one of Brazil's most severely deforested regions, have recorded at least 551 tree species (*69*). Another 766 species have a high probability of occurring at Cristalino according to our model, and as many as 1214 of the 1317 species known or expected from Cristalino qualify as globally threatened under the BAU. Similar analyses could help ensure that Amazonian protected areas with especially high numbers of globally threatened tree species receive the levels of protection and funding they merit.

Many practical and scientific obstacles stand in the way of a stable, comprehensive red list for Amazonian tree species. What our study showed is that such a list will include several thousand species, many of which are currently considered common, and will include a very large majority of the tree species occurring in the Amazon's worst-hit regions. As Amazonian forest loss continues, new approaches such as these will be needed to help guide management away from business-as-usual scenarios and ensure a long-term future for the world's richest tree flora. Indeed, sustaining the recent historical trend of reduced Amazonian deforestation through 2050 will keep as many tree species from becoming Critically Endangered as there are Critically Endangered plant species on the IUCN Red List today.

The future of my work in the Amazon

The work with the Amazon Tree Diversity Network has been very fruitful. Despite the limitations of our data (unknown species (*70*), unidentified material), the small sample size, considering the Amazon area, we have made great steps in our knowledge of this area. Much work is still ongoing. Current projects include: Phylogenetics of the Amazon trees (lead Kyle Dexter, Edinburgh, UK); Importance of floodplains for Amazon diversity (lead Florian Wittmann, Karslruhe, Germany); (Mono)dominance in the Amazon (Lead Daniel Sabatier, Montpellier, France; Ben & Bia Marimon, Nova Xavantina, Brazil; Hans ter Steege, Leiden, NL); Modelling of species in a changing Amazon (Lead: Vitor Gomes, Belém, Brazil); The role of dispersal in determining diversity in the Amazon (lead Edwin Pos, Utrecht, NL); Functional Diversity in the Amazon Rain Forest (lead Hans ter Steege, Jésus Aguirre Gutierrez, Leiden, NL).

I am also coordinating work with other plot networks: Atlantic forest network (lead: Renato Lima, USP, Sao Paulo); Andes forest network (Lead: Miles Silman, US); Amazon Epiphyte Network (Lead Charles Zartman, INPA, Manaus, Brazil); Modelling forest composition (PhD proposal Iris Hordijk, Hans ter Steege, Lourens Poorter).

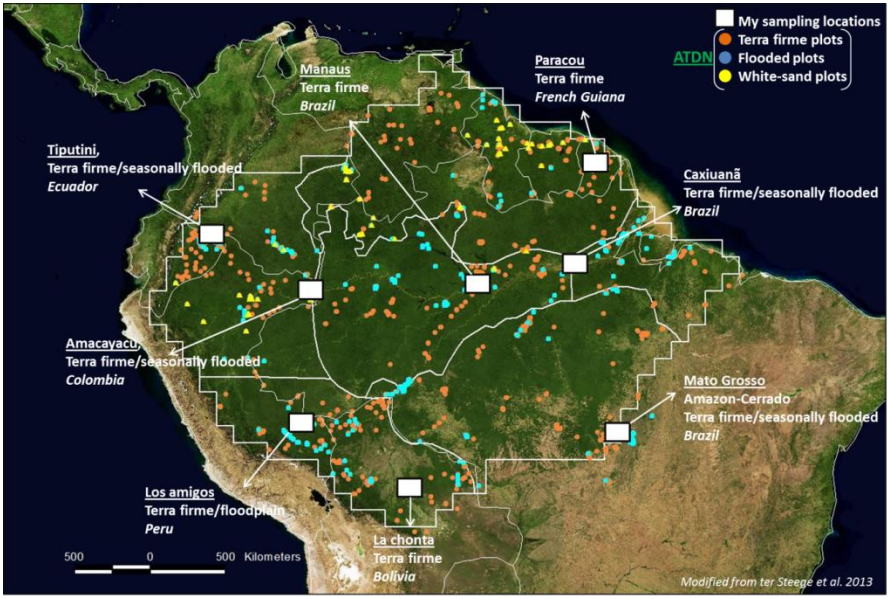

Figure 7. Possible sites for more intensive research.

ATDN has brought us much information on large spatial scales. On a few selected sites (Fig. 7), well chosen to cover the main fertility and rainfall gradients we intend to study the forest more intensely, focusing on species interactions (using next generation sequencing techniques), linking biodiversity with structural and functional diversity (using Lidar and remote sensing techniques) and population genetics. I also hope that more ecosystem studies (such as log-life) can be executed here.

I will keep collaborating within the RAINFOR Network studying the carbon storage and dynamics of the Amazon forest. Also within this Network work has shifted towards the effect of climate on species distribution and towards evolution.

Personally, I would like to delve in the link between speciation and abundance of species. Our work showed that hyperdominants are mainly found in species-poor taxa. Speciation thus leads to a reduction in abundance. Some genera are hyperdominant as genus but have very few hyperdominant species. I am curious how this should work and if hyperdominants have always been hyperdominants. New Bayesian coalescence techniques may help us to solve these questions.

Acknowledgements
I want to thank my parents for their care and upbringing. I am truly sorry my father cannot be present here today. Apart from Walt Disney, his love for nature and our weekly very early morning walks into 'Het Brunnink's Hof', to see the roe deer, certainly helped to foster a fieldwork mind. Later, I spent many days with my friend exploring 'het Haaksbergerveen' and many moors across the border in Germany.

I thank my brother and sisters for their warmth and care for their little and big brother. Together we had a great youth, except of course during dish washing.

Arua and Duane, you have had a youth part in Guyana and part in the Netherlands in a period where my work was busy and you had to share me with that forest. I hope I have been enough father and not too much away. Thanks for being here.

Sylvia, I am so happy we met. We were both in difficult times and somehow a perfect match, and despite coming from different continents, culture and religion, we share a lot of values. I also value your sharp analytical mind and great skills in formulating text. Thanks Maria, Daniel and my new family in Brazil for love, warmth and a new home, away from home.

All my colleagues, PhD students and MSc students with whom I worked together at the Utrecht University, The Tropenbos-Guyana Programme, Tropenbos International, the International Institute for Geo-Information Science and Earth Observation and

Naturalis Biodiversity Center, thanks for your enthusiasm, support and discussions. Special thanks to my promotor Marinus Werger, whose unwavering support and critical pen have been instrumental in my career. Special thanks also to Han Wösten and Erik Smets who made my transition from Utrecht University to Naturalis a reality.

Last but not least, thanks to Hans Cornelissen and Rien Aerts for their efforts to create the chair in 'Tropical Forest Diversity and Tree Traits', which I am now officially accepting with this speech.

Ik heb gezegd.

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